thought might serve for diffusion of substrates and products.[17] As shown in the top half of Figure 6.3, in 1953 both men produced 3D models – Palade a wax model and Sjöstrand a diagram – that illustrate the differences in how they conceived of these structures. Note especially the area in Palade's model labeled *fc* (for *central free channel*, later called the *mitochondrial matrix*). The two sketches in the bottom half of Figure 6.3 schematically illustrate a medial longitudinal section through each 3D model (discussed below).

The controversy between Sjöstrand and Palade was often personal and acrimonious.[18] Sjöstrand argued vociferously for the higher quality of his micrographs and for artifacts in Palade's micrographs. In particular, at the Third International Conference on Electron Microscopy, held in London in 1954, he proposed that the appearance of an open channel in the middle of mitochondria in Palade's micrographs was due to poor preservation as a result of delays in fixing the specimens (Sjöstrand, 1956b). These delays, he alleged, led to swelling during the postmortem interval before fixation was complete. To demonstrate the process he thought gave rise to Palade's micrographs, he prepared a series of micrographs at different intervals and claimed that the later micrographs showed increasing disruption of the internal membranes:

> Studies of post-mortem changes taking place within 15–30 to 45 minutes after death have shown that the mitochondria are changed very soon after death. They swell after the shutting off of the blood supply, the inner mitochondrial membranes appear fragmented and pulled apart leaving a more or less extensive central space free from inner membranes. It might be that such postmortem changes are responsible for the central space described by Palade. (Sjöstrand, 1956a, p. 463)

Sjöstrand maintained that a primary factor in generating high-resolution micrographs was keeping the tissue in as life-like a condition as possible. Thus, he injected fixative directly into living animals and as quickly as pos-

[17] In his 1952 paper Palade had commented, "In longitudinal sections that cut close to the mitochondrial membrane, the appearance of the lamellae might suggest that they are septa that traverse the mitochondrion from side to side. Oblique sections, however, indicate that the lamellae are actually ridges or folds protruding from the inside surface of the mitochondrial membrane towards the interior of the organelle without reaching the other side" (p. 432).

[18] At least in the eyes of Keith Porter, Sjöstrand's success was derivative from his and Palade's efforts. He complained to Pomerat that Sjöstrand failed to sufficiently acknowledge the assistance he had received. Yet, in his paper with Rhodin on the ultrastructure of mouse kidney tubules Sjöstrand says, "We feel very much indebted to Dr. K. Porter and to Dr. G. E. Pallade [employing the original spelling for Palade's name] for their kindness in giving the necessary information regarding the fixation technique used in the investigation. During the printing of this paper the paper by G. E. Pallade describing the fixation technique in *J. Exptl. Med.* **95**, 285 (1952) has become known to us" (Sjöstrand & Rhodin, 1953, p. 427, n. 1).